# Genotype and Environment Variation for Arabinoxylans in Hard Winter and Spring Wheats of the U.S. Pacific Northwest

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**ABSTRACT**

The development of high-quality wheat (*Triticum aestivum* L.) cultivars depends on a thorough understanding of the constituents of grain and their variation due to genetics and environment. Arabinoxylans (pentosans) are key constituents of wheat grain and have broad and far-reaching influences on milling and baking quality. However, variation in arabinoxylans due to genotype and environment are not fully understood. In this study, 25 hard winter and 25 hard spring wheat commercial cultivars and advanced breeding lines developed from eight public and private breeding programs in the U.S. Pacific Northwest were analyzed for water-extractable and total arabinoxylan contents (WE-AX and total AX), and the proportion of total AX that was water-extractable. Winter and spring genotypes were grown in three environments each. The results indicated that there were significant differences among both sets of hard wheat genotypes for WE-AX, total AX, and proportion of total AX that was WE-AX. The WE-AX and total AX mean content ranges for the winter cultivars were 0.390–0.808 and 3.09–4.04%, respectively; and for the spring cultivars 0.476–0.919 and 3.94–4.70%, respectively. WE-AX as a percentage of total AX was similar between the two genotype sets, 11.7–23.0%. Arabinoxylan fractions were generally not correlated with grain protein, test weight, and kernel hardness. The two highest correlations for winter wheats were between protein and total AX ($r$ = –0.40) and test weight and percentage of total AX that were water-extractable ($r$ = 0.37) for winter wheats. Among spring wheats, single-kernel characterization system hardness was negatively correlated with WE-AX and proportion of total AX that was WE-AX ($r$ = –0.46 and –0.51, respectively). Although often significant, arabinoxylan fractions were usually not highly intercorrelated, indicating some independence of traits. Notable genotypes, being especially high or low for one or more arabinoxylan fraction and, thus, candidates for further genetic study and cross-breeding, included Juniper, Eddy, and ORN980995 winter wheats, and Hollis, Alta Blanca, and WQL9HDALP spring wheats. Although the results indicate that arabinoxylan fractions of wheat grain can be highly influenced by environment, there is clear support for the existence of genetic differences, especially for WE-AX and the proportion of total AX that is water-extractable. As such, the manipulation of arabinoxylan content of wheat grain seems to be a reasonable breeding objective.

The biochemical constituents of wheat (*Triticum aestivum* L.) grain largely determine its end-use quality. One such important constituent is a group of nonstarch polysaccharides referred to collectively as pentosans. More specifically, a major member of the pentosan family, albeit a minor constituent in grain overall, is a highly heteromorphic group of polymers known as arabinoxylans. Arabinoxylans comprise (1→4)-β-xylan chains variously substituted at the O-2 and O-3 atoms, most commonly with α-L-arabinofuranosyl residues (Fincher and Stone 1986; Ordaz-Ortiz et al 2005). The pattern of arabinose substitution, which includes frequency, regularity, O-2 versus O-3, and mono- versus di-substitution, as well as other minor residue substitutions, confers important differences in the physicochemical properties of the arabinoxylans and, consequently, their influence on wheat grain and flour quality. Perhaps the most important additional substitution involves ferulic acid esterified at the O-5 position of the arabinose residue.

Arabinoxylans are constituents of cell walls. In wheat endosperm and aleurone tissues, arabinoxylans constitute ≈65–70% of the polysaccharide present in cell walls, with cellulose representing <5% (Fincher and Stone 1986). In contrast, the cell walls of bran and the outer layers of the pericarp contain ≈60% arabinoxylan or glucuronoarabinoxylan and 30% cellulose. In total, the outer tissues of the kernel that compose bran are especially rich in arabinoxylans and may exceed 20–30% by weight (Hashimoto et al 1987; Wang et al 2006), with individual layers such as outer pericarp as high as 48% (Barron et al 2007). Consequently, differential flour milling performance among cultivars (e.g., flour yield or extraction, bran shattering and contamination, endosperm-bran separation, etc.) will confound the relationship between grain and flour arabinoxylan. Here, we focus on only whole-grain arabinoxylan content.

Arabinoxylans may be classified according to solubility, extractability, or fractionation procedure (Courtin and Delcour 2002). Total arabinoxylan (total AX) content is often subdivided into two solubility classes: water-extractable (WE-AX) (water-extractable is used in preference to water soluble) and water-unextractable. Henry (1985) examined grain of two wheat cultivars and found 0.87 and 1.5% WE-AX and 6.2 and 7.1% total AX. Henry (1987) subsequently reported similar values of 6.2–6.9% total AX. Hashimoto et al (1987) reported that a sample of Centurk 78 hard red winter wheat cultivar from a single Kansas site contained 0.68% WE-AX and 6.7% total AX; these values were adjusted to 0.90 and 9.0%, respectively, for extraction efficiency and moisture content. Hong et al (1989) studied seven hard red winter and hard white winter cultivars, seven soft white winter cultivars, and four soft white club cultivars from a single Washington location. WE-AX was 0.31–0.76% and total AX was 4.1–6.1%. By including a second markedly different Washington environment, they calculated the genotype-to-environment variance ratio ($\sigma_{genotype}/\sigma_{environment}$) to be 1.6 for WE-AX and 2.4 for total AX. Saulnier et al (1995) examined 20 wheat cultivars grown in France and found that WE-AX was 0.36–0.83% and total AX was 5.5–7.8% using two assay methods (GLC of alditol acetates and phloroglucinol). The two assay methods agreed quite well, with phloroglucinol giving, on average, slightly higher values. Martinant et al (1998) studied the arabinoxylans in two genetic mapping populations: Courtout × Chinese Spring ($n$ = 91 doubled haploids, two crop years; year 1 was whole meal and year 2 was ≈70% extraction Quad Jr. flour yield) and Synthetic × Opata ($n$ = 76 recombinant inbred lines, 1 crop year, ≈70% flour extraction Quad Jr.). The range of WE-AX over the entire set of lines for Courtout × Chinese Spring was 0.22–0.70% and for Synthetic × Opata was 0.34–0.79%. In a subsequent report (Martinant et al 1999), this group measured WE-AX in Quadrumat Sr. white

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flours (≈70% extraction) derived from 19 cultivars grown in three locations in France in one year and 16 cultivars grown at one location in a second year. WE-AX was 0.26–0.91%, with a broad-sense heritability coefficient ($h^2$) ($\sigma^2_{genotype}/\sigma^2_{genotype} + \sigma^2_{environment}$) of 0.75. Ordaz-Ortiz et al (2005) found a range of 4.8–6.9% total AX among 20 wheat cultivars grown at a single site in France. Zhang et al (2005) examined 17 soft wheat genotypes and reported that both genotype and environment were important sources of variation but that genotype was the most important for water-soluble pentosan. The genotype × environment interaction was not significant. Wang et al (2006) reported that six hard spring wheat cultivars had total AX contents of 5.5–7.3% and WE-AX contents of 0.62–0.90%. Finnie et al (2006) studied seven soft white spring wheat cultivars grown in 10 unique environments and 20 soft white winter wheat cultivars grown in 12 environments. The range for the soft white spring samples was 0.29–0.91% WE-AX and 3.2–6.1% total AX. The soft white winter samples had a similar range of 0.24–0.74% WE-AX and 3.1–6.4% total AX, suggesting that genetic and environmental contributions might be similar for both groups of cultivars. Individual cultivar means ranged from 0.42% WE-AX for the spring club cv. Eden to 0.67% for Alpowa soft white spring. The cultivar with the lowest total AX content was Hiller winter club (3.7%) and the highest was again Alpowa soft white spring (4.7%). Barron et al (2007) reported total AX contents of 5.3 and 6.5% for two wheat cultivars. Jiang et al (2007), using six genotypes and five environments, found that genotype influenced pentosan content most but that environment and the genotype × environment interaction were also significant. Dornez et al (2008a) reported that, among 14 wheat cultivars grown in three years, the WE-AX content ranged nearly twofold, 0.42–0.99%; total AX was 5.81–7.56%. They considered the range in total AX to be limited. Among a subset of six cultivars grown in all three years, the genotypic variance for total AX was 18% whereas crop year had no significant effect. However, the genotype × year interaction accounted for 35% of the variance. WE-AX varied more among genotypes than did total AX. In contrast to total AX, they found that WE-AX levels were highly correlated across crop years and genotypic variance was 57%; crop year variance was 37%. In this case, the interaction was negligible.

Coles et al (1997) found that the arabinoxylan content of wheat cv. Batten increased with drought but was not affected by nitrogen. Lempereur et al (1997) examined the arabinoxylan content of five durum (*T. turgidum* subsp. *durum*) cultivars grown at two sites in France under four different agronomic conditions, including irrigation and nitrogen fertilizer regimes. Mean WE-AX for cultivars was 0.37–0.56% and total AX was 4.1–6.0%. Given their experimental design, they calculated genotype, environment, and residue variation percentages as 58.8, 11.9, and 29.3%, respectively, for WE-AX and 73.0, 16.0, and 10.9%, respectively, for total AX. The genotype × environment ratio ($s^2_{genotype}/s^2_{environment}$) was 4.9 and 4.4, WE-AX and total AX, respectively. Li et al (2002) and Wang et al (2006) found that environment (including management practices) had a relatively greater influence on pentosan (arabinoxylan) content compared with genotype, although some genotype differences were found. Dornez et al (2008b) reported that fungicides and nitrogen fertilizer rates had no effect on either WE-AX or total AX contents. Delaying harvest up to one month had no effect on total AX but increased WE-AX, ostensibly due to sprouting and endoxylanase activity.

Numerous studies have examined the influence of arainoxylans on dough mixing, baking, and wheat and flour end-use quality. However, few studies have examined specifically the contribution of genotype (cultivar) to variation in arabinoxylan content of grain and compared that contribution to the role that environment may play. Understanding the sources of variation in WE-AX and total AX contents and the proportion of total AX that is water-extractable is useful to wheat-breeding programs where the aim is to develop new wheat cultivars with superior and consistent end-use quality. The objective of this study was to investigate the influence of genotype and growing environment on grain arabinoxylan content in a comprehensive survey of commercial cultivars and advanced breeding lines of U.S. Pacific Northwest hard wheat, including red and white bran, and winter and spring growth habit types.

## MATERIALS AND METHODS

### Hard Red and White Wheat Meal Samples

Hard red and hard white wheat samples were obtained from an ongoing genotype and environment study conducted by the United States Department of Agriculture, Agricultural Research Service Western Wheat Quality Laboratory in Pullman, WA. Depending on growth habit (winter or spring), the samples were organized and grown in two sample sets by the Washington State University Cereal Variety Testing (WSUCVT) program. An equal number of winter and spring wheat cultivars were included. The winter sample set contained 25 hard wheat genotypes: ACS51084, Bauermeister, Darwin, Eddy, Finley, Hatton, ID621, ID641, Juniper, KKHWWW05, MDM, ORN00B507, ORN00B553, ORN98-0995, AgriPro Paladin, AgriPro Palomino, W98-344, WA-7975, WA7976, WA7977, WA8001, WA8002, WA8003, WA8004, and Weston; and additionally included the soft white winter wheat check cv. Eltan, which is the overall leading cultivar in the state of Washington. All cultivars were grown together at WSUCVT program locations near Connell (46°37.2N, 118°43.6W, elevation 380 m), Horse Heaven (46°7.6N, 119°40.2W, elevation 306 m), and Pullman (46°41.7N, 117°7.7W, elevation 747 m), Washington and harvested in 2006. The spring sample set contained 25 hard wheat cultivars: ACS52610, Alta Blanca, Blanca Grande, BZ903-455WP-D, BZ999-339, BZ9M03-1044, Hollis, Otis, ID377s, Macon, Scarlet, Tara2002, WA7953, WA7954, WA7990, WA7998, WA8010, WA8012, WA8015, WA8016, WA8017, WA8018, WB-926, Winchester, and WQL9HDALP, all grown together and harvested in 2006 from WSUCVT program locations near Almira (47°49.0N, 118°51.9W elevation 704 m), Dayton (46°15.2N, 117°59.4W elevation 658 m), and St. John (47°4.8N, 117°31.2W, elevation 665 m), Washington. All winter and spring locations were rain-fed (crop year precipitation): Connell (350 mm), Horse Heaven (265 mm), and Almira (400 mm) were summer fallow and Pullman (530 mm), Dayton (510 mm) and St. John (525 mm) were annual cropped. WSUCVT program nursery mean yields over all entries were Connell, 4.2 t/ha; Horse Heaven, 3.0 t/ha; Pullman, 8.9 t/ha; Almira, 4.7 t/ha; Dayton, 4.4 t/ha; and St. John, 5.0 t/ha. All samples were of commercial quality, with test weight of 764–846 kg/hL (mean 815 kg/hL), and protein content (12% moisture basis) of 95.3–169.1 g/kg (mean 132.0 g/kg).

Test weight was measured according to Approved Method 55-10 (AACC International 2000) and the units converted. Single-kernel characterization system (SKCS) 4100 grain hardness was conducted according to Approved Method 55-31. All wheat samples (50 g each) were ground (no tempering) into meal with a cyclone mill (Udy, Boulder, CO) through a 0.5-mm screen. The resulting meals were analyzed for moisture content (Approved Method 44-16), which was 9.0–10.0%. Meal nitrogen content was determined by the Dumas combustion method (Approved Method 46-30) (model FP-428, Leco Corp., St. Joseph, MI); protein was calculated as nitrogen × 5.7 and reported on a 12% moisture basis.

### Arabinoxylan Determination

A colorimetric method described by Douglas (1981) that measures pentose sugar content in wheat flour was modified to measure both WE-AX and total AX content from wheat meal. Modifications to the Douglas (1981) method followed those described in detail by Finnie et al (2006). Briefly, 125 mg of meal

was placed in a 50-mL tube to which was added 25 mL of water. The samples were suspended by vortexing, and 1 mL of sample suspension was quickly removed into a reaction tube and used to determine total AX content. The original sample suspension was extracted for 30 min and centrifuged, and 1 mL of supernatant was removed and placed into a stoppered reaction tube for determination of WE-AX content. For each meal sample, two sample suspensions were made and, from each sample suspension, two assays were conducted for WE-AX and total AX contents. A standard curve was produced using a stock solution of 10 mg of D-(+)-xylose (X-1500, Sigma) in 100 mL of water with triplicate standard samples at each dilution (Finnie et al 2006). Standard check samples were analyzed with each batch of meal samples. Arabinoxylan content was calculated after the equation provided by Finnie et al (2006).

### Statistical Analysis

The two assays from each sample suspension for total AX and supernatant for WE-AX were considered repeated measures and were averaged; the two independent aliquots of ground meal were considered statistical replicates of each grain lot. The WE-AX to total AX ratio was calculated for each meal replicate. Analysis of variance (ANOVA) was conducted using Proc GLM (SAS Institute, Cary, NC) separately for the winter and spring wheat genotype sets with a factorial model with genotypes (G), environments (E), and the G × E interaction term. Genotype and environment were considered fixed effects. Model component *F* tests were performed using type III mean squares. Variance ratios, $\sigma_{genotype}/\sigma_{environment}$ and $\sigma_{genotype}/\sigma_{genotype \times environment}$, were calculated using type III mean squares. Mean separation was determined using Duncan's Multiple Range Test (DMRT) at $\alpha = 0.05$ (least significant difference is equal to the DMRT critical value for two adjacent means). Pearson correlation coefficients were calculated using PROC CORR (SAS Institute) on grain lot means (i.e., AX measures were average over replicates).

## RESULTS

For both classes of genotypes (winter and spring), both fractions of arabinoxylan (WE and total), and the proportion of WE-AX of the total AX, the ANOVA models appeared robust in that they explained 64–96% of the total variation in grain arabinoxylan content (Table I). For WE-AX, the models indicated similar variation between the winter and spring wheats. For total AX, however, the winter and spring genotype sets were dissimilar; the difference in the whole model $R^2$ and *F* values appeared to be mostly due to the similarity among the three spring wheat environments. Whole-model mean square errors were similar (0.070 and 0.081, winter and spring, respectively), as were the genotype model component mean squares (0.380 and 0.245, winter and spring, respectively). However, the environment model component mean squares for winter wheats was 13.0 whereas for the spring wheat set it was only 0.124; the spring wheat value was not significant (Table I). Environment means supported this conclusion (Table II). The difference between means of the high and low environments was 0.188% for WE-AX of winter genotypes and 0.156% for WE-AX of spring genotypes, but 1.00% for total AX of winter genotypes and only 0.10% for total AX of spring wheat genotypes (Table II). Of interest, the three environments reversed rank order between WE-AX and total AX for the winter wheat genotypes. It would appear from these results that environmental effects on arabinoxylan fractions are not consistent and may affect the WE-AX and total AX fractions differently.

Returning to the ANOVA results (Table I), the environments under which the winter wheat genotypes were grown were a much greater source of variation for WE-AX and total AX contents compared with genotype. For the spring wheat set, environment was again much more influential for variation in WE-AX (Table I). The G×E interaction ANOVA model term was notably small for WE-AX of both winter and spring genotypes but was more similar to the genotype *F* value for total AX among the winter wheats. Like the environment model component for the spring total AX, the G×E component was also not a significant source of variation.

The proportion (percentage) of WE-AX as a function of the total AX in the wheat grain was calculated and its variation analyzed (Table I). For the winter genotypes, the percentage of WE-AX varied most according to environment. For the spring wheat genotypes, the environment was also the greatest source of variation. Although the interaction terms for both winter and spring wheat sets was significant, the main effect model components were considerably larger.

**TABLE I**
**Analysis of Variance Whole Model $R^2$ Values, *F* Values, and Variance Ratios of Water-Extractable (WE-AX), Total Arabinoxylan (AX), and WE-AX as a Percentage of Total AX (WE/Total) in U.S. Pacific Northwest Hard Winter and Spring Wheat Genotypes[a]**

| | Winter Genotypes | | | Spring Genotypes | | |
|---|---|---|---|---|---|---|
| **Source** | **WE-AX** | **Total AX** | **WE/Total** | **WE-AX** | **Total AX** | **WE/Total** |
| Whole model $R^2$ | 0.95 | 0.90 | 0.95 | 0.96 | 0.64 | 0.91 |
| Whole model *F* value | 17.2*** | 9.0*** | 20.9*** | 23.4*** | 1.8** | 9.7*** |
| Genotype (G) *F* value | 24.0*** | 5.4*** | 12.0*** | 48.5*** | 3.0*** | 19.2*** |
| Environment (E) *F* value | 179.4*** | 185.5*** | 523.4*** | 158.4*** | 1.5ns | 67.9*** |
| G × E *F* value | 7.0*** | 3.8*** | 5.1*** | 5.2*** | 1.2ns | 2.5** |
| $\sigma_G/\sigma_E$ | 0.13 | 0.03 | 0.02 | 0.31 | 1.98 | 0.28 |
| $\sigma_G/\sigma_{G \times E}$ | 3.44 | 1.43 | 2.37 | 9.35 | 2.61 | 7.65 |

[a] *F* values and variance ratios used type III mean squares; ns, $P > 0.05$; *, $P < 0.05$; **, $P < 0.01$; and ***, $P < 0.001$.

**TABLE II**
**Environment Mean Water-Extractable (WE-AX), Total Arabinoxylan (AX), and WE-AX as a Percentage of Total AX (WE/Total) in U.S. Pacific Northwest Hard Winter and Spring Wheat Genotypes[a]**

| | Winter Genotypes | | | | Spring Genotypes | | |
|---|---|---|---|---|---|---|---|
| **Environment** | **WE-AX (%)** | **Total AX (%)** | **WE/Total (%)** | **Environment** | **WE-AX (%)** | **Total AX (%)** | **WE/Total (%)** |
| Connell | 0.692a | 3.08a | 22.7a | St. John | 0.789a | 4.30a | 18.3a |
| Horse Heaven | 0.571b | 3.63b | 15.7b | Almira | 0.727b | 4.20a | 17.3b |
| Pullman | 0.504c | 4.08c | 12.4c | Dayton | 0.633c | 4.24a | 15.0c |
| $LSD_{(0.05)}$ | 0.020 | 0.10 | 0.65 | $LSD_{(0.05)}$ | 0.018 | ns | 0.59 |

[a] Values followed by the same letter are not significantly different ($P < 0.05$); LSD, least significant difference.

Variance components were used to examine in a different way the relative contribution of G, E, and G×E to genotypic differences in grain arabinoxylans. The ratio of G-to-E variation ($\sigma_{genotype}/\sigma_{environment}$, $\sigma_g/\sigma_e$) was calculated using the type III mean squares and is presented in Table I. The small $\sigma_g/\sigma_e$ values for the winter genotypes, considerably less than one for WE-AX, total AX, and the proportion of WE-AX of the total AX, reflect the relatively much larger contribution from the environment.

The ratio of the genotype variance to the G×E interaction ($\sigma_{genotype}/\sigma_{genotype-environment}$, $\sigma_g/\sigma_{g-e}$) provided an indication of the relative stability of the genotypes across environments. The value of $\sigma_g/\sigma_{g\times e}$ for WE-AX for the winter genotypes suggests that repeated testing across environments for this arabinoxylan fraction may be useful for obtaining meaningful results because the trait was influenced somewhat differentially depending on the specific environment under which the genotypes were grown. A visual inspection of the genotype means plotted against the three locations indicated considerable cross-overs (data not shown). For total AX, however, the ratio was even smaller, 1.43. When WE-AX was calculated as a function of total AX, the ratio was 2.35, indicating that, in addition to a large environmental effect (see above), the genotypes performed somewhat consistently across environments.

For the spring wheat genotypes, the $\sigma_g/\sigma_e$ ratio for WE-AX was again considerably less than one, whereas the ratio for total AX was nearly two. The higher value for total AX likely reflects the nonsignificant differences among the three environments. The ratio for WE-AX as a function of total AX was also considerably less than one. The $\sigma_g/\sigma_{g\times e}$ for spring wheats was especially large for WE-AX (9.35) and the proportion of WE-AX of the total AX (7.65). For total AX, the value was 2.61. In all three cases, these results may be more reflective of the smaller amount of environmental variation present.

Returning to Table II, highly significant differences were observed among the winter wheat locations for WE-AX, total AX, and the proportion of WE-AX of the total AX. Connell and Horse Heaven are dry, lower-yielding locations and had the higher levels of WE-AX but lower levels of total AX, whereas Pullman is a higher-rainfall, high-yielding environment and had low WE-AX but the highest total AX (agronomic information as above). As a proportion of total AX, Connell had the highest percentage of WE-AX (22.7%), whereas the other two environments were less at ≈12 and 16%. The spring wheat locations were less diverse with similar mean grain yields (≈4.5–5.0 t/ha). Although Almira had considerably less precipitation in 2006, it was farmed as summer fallow and therefore probably had similar soil moisture available for crop development (as evidenced by the mean grain yield). However, the WE-AX did differ among the spring wheat environments but the ranking did not follow any discernable pattern relative to general yield or precipitation. WE-AX as a proportion of total AX ranged from 15.0% at Dayton to 18.3% at St. John. The range was less than that for winter wheat genotypes but all were significantly different (Table II). Clearly, more studies will be needed to better ascertain the relationships between environmental factors and arabinoxylan fractions in grain.

Grain protein content and test weight are two traits that can be highly affected by the environment and management. To see if these traits and SKCS hardness had any relationship to arabinoxylans, Pearson correlation coefficients ($r$) were calculated among the following parameters: WE-AX, total AX, proportion of total AX that was water -extractable, grain protein content, test weight, and SKCS hardness (Table III). For the winter wheat set, grain protein content was significantly negatively correlated with total AX and significantly positively correlated with WE-AX and the percentage of total AX that was water-extractable, indicating that, among these grain samples, higher protein was related to lower total AX, with a greater proportion that was water-extractable. Protein content was not correlated with any arabinoxylan fraction among the spring wheat genotype set. Test weight showed a modest positive relationship with WE-AX for both winter and spring wheat genotypes ($r$ = 0.24 and 0.21, winter and spring, respectively; $P$ values were 0.04 and 0.07, respectively). For the winter wheat set, test weight was also correlated with percentage of WE-AX as a function of total AX ($r$ = 0.28, $P$ = 0.02). SKCS hardness was not significantly correlated with any of the three AX fractions for winter wheats. However, for spring wheats SKCS hardness was significantly negatively correlated with both WE-AX ($r$ = –0.46) and proportion of total AX that was water-extractable ($r$ = –0.51). In summary, arabinoxylans, in general, do not appear to be related to either grain protein or test weight or highly influenced by the same environmental or management parameters that result in variation in these grain traits. SKCS hardness was not correlated with AX fractions in winter wheat but was negatively correlated with the WE fractions in the spring wheat set.

Among the three arabinoxylan fractions, the absolute quantity of WE-AX was highly correlated with the percentage of WE-AX as a function of total AX (Table III). Any other correlation was specific to either the winter or spring wheat set. For winter wheats, the percentage of WE-AX decreased with increasing total AX whereas, among the spring wheats, this correlation was not significant. Alternatively, for the spring wheats, the WE-AX increased with increasing total AX but in the winter wheat set, this correlation was not significant.

We have particular interest in potential differences among genotypes for arabinoxylan fractions from both a grain utilization standpoint and a genetic/biosynthetic viewpoint. The mean WE-AX, total AX, and the percentage of WE-AX of total AX across the three common environments for each set of genotypes are

**TABLE III**
**Correlation Coefficients ($r$) and $P$ Values Among Arabinoxylan Fractions, Test Weight, Grain Protein, and Single-Kernel Characterization System (SKCS) Hardness for U.S. Pacific Northwest Hard Winter (upper right diagonal) and Hard Spring (lower left diagonal) Wheat Genotypes[a]**

| | WE-AX | Total AX | WE/Total | Test Weight | Wheat Protein | SKCS Hardness |
|---|---|---|---|---|---|---|
| WE-AX | … | –0.09 | 0.83 | 0.24 | 0.21 | 0.12 |
| | | (0.45) | (<0.0001) | (0.04) | (0.06) | (0.30) |
| Total AX | 0.44 | … | –0.60 | –0.09 | –0.40 | 0.02 |
| | (<0.0001) | | (<0.0001) | (0.46) | (0.0003) | (0.84) |
| WE/Total | 0.96 | 0.17 | … | 0.27 | 0.35 | 0.10 |
| | (<0.0001) | (0.15) | | (0.02) | (0.002) | (0.38) |
| Test Weight | 0.21 | 0.11 | 0.19 | … | 0.14 | 0.04 |
| | (0.07) | (0.34) | (0.10) | | (0.22) | (0.71) |
| Wheat Protein | 0.16 | 0.04 | 0.16 | –0.22 | … | –0.22 |
| | (0.17) | (0.75) | (0.16) | (0.06) | | (0.05) |
| SKCS Hardness | –0.46 | 0.03 | –0.51 | –0.06 | 0.05 | … |
| | (<0.0001) | (0.83) | (<0.0001) | (0.59) | (0.67) | |

[a] WE-AX, water-extractable arabinoxylan; total AX, total arabinoxylan; WE/total, water-extractable arabinoxylan as a percentage of total arabinoxylan; for each correlation, the upper number is the coefficient ($r$) and the lower number (in parenthesis) is the level of significance ($P$).

provided in Tables IV and V. WE-AX of the winter wheat genotypes were more than twofold from a low of 0.390% for the Oregon State University breeding line ORN980995 to a high of 0.808% for Juniper (Table IV). DMRT was used to identify the genotype means that differed significantly from one another. The genotypes assorted themselves into a considerable number of DMRT groups. Juniper was distinctly higher than all other genotypes and may be of notable interest for a genetically high level of total AX. At the lower end of the range, Eddy and ORN00B507 were not significantly different from the lowest genotype, ORN980995. Of the winter genotypes currently grown as commercial cultivars (2007 harvest data from the National Agricultural Statistics Service), Bauermeister was most widely grown with 37 kha, followed by Eddy (33 kha) and Finley (25.5 kha), all in Washington. AgriPro Paladin ranked number 4 in Washington (14 kha). The leading hard winter wheat cultivar in both Idaho and Oregon was Boundary (24 and 4.5 kha, respectively). Boundary ranked eighth overall for hard winter cultivars in Washington (6 kha). All of these cultivars are hard red winter wheat. They generally spanned most of the range observed for WE-AX (Table IV). The hard white winter genotypes clustered near the center of the distribution from ID641 to Darwin. Eltan, a soft white winter wheat, had 0.653% WE-AX, which placed it in the upper range. Of note, Bauermeister is a hard red back-cross derivative of Eltan; MDM is a hard white back-cross derivative of Eltan (Jones et al 2007a,b).

For total AX, the range extended from ORN980995 (3.09%) to WA8002 (4.04%) (Table IV). Groupings tended to be larger with greater overlap than for the WE-AX. For example, the lowest DMRT group (j) which began with ORN980955 included seven genotypes; the highest DMRT group (a) included 11 genotypes. However, all genotypes in these two respective groups were judged by DMRT to be significantly different from each other (that is, all genotypes in the low group were significantly different from all genotypes in the high group). The hard white genotypes ranged from Darwin up to MDM; Darwin and ID641 were significantly lower than MDM (note DMRT groups c and f). Eltan, the soft white winter genotype, appeared in the highest DMRT group.

After calculating the proportion of WE-AX as a function of the total AX grain content, DMRT indicated similar differences among the winter genotypes (Table IV). In this case, Eddy was the lowest, with 11.7% of its total AX being present in the WE fraction. Juniper was the highest, with nearly twice as much, 23.0%, of its total AX being present in the WE fraction. Again, Eddy was lowest and significantly different from all other genotypes, followed by the next lowest, ORN00B553. Juniper was significantly higher than all other genotypes, followed by the next highest, Finley.

WE-AX for the spring wheat genotypes ranged from a low of 0.476% for Alta Blanca to a high of 0.919% for Hollis, again nearly a twofold difference (Table V). DMRT was used to test mean differences. Interestingly, the spring wheat genotypes tended to form clusters for WE-AX. The highest (a) DMRT group had Hollis, WA7954, Blanca Grande, and BZ999-339. The first three of these genotypes were significantly higher than all others except WB926 (b group). There was a more distinct discontinuity in the distribution of genotypes for WE-AX between WA8015 (lowest of i group, 0.693%) and Scarlet (highest of j group, 0.613%). Alta Blanca was significantly different from all other spring wheat genotypes (l group, 0.476%), a full 0.063% less than the next lowest, ACS52610.

Of the spring wheat genotypes currently grown as commercial cultivars (2007 harvest data from the National Agricultural Statistics Service), the WestBred hard red spring cvs. WB926 and WB936 are the most widespread; together, they accounted for 61.5 kha in Idaho and 17 kha in Washington. The arabinoxylan content of WB936 is unknown. WB926 had a WE-AX content in the upper range (Table V). Other leading commercial cultivars, Jefferson (no. 2 hard red spring wheat cultivar in Idaho, no. 1 in

**TABLE IV**
**Water-Extractable (WE-AX), Total Arabinoxylan (AX), and WE-AX as a Percentage of Total AX (WE/Total) of U.S. Pacific Northwest Hard Winter Wheat Genotypes[a]**

| Genotype | WE-AX (%) | Total AX (%) | WE/Total (%) |
|---|---|---|---|
| Juniper | 0.808a | 3.59a–g | 23.0a |
| Finley | 0.739b | 3.69a–g | 20.3b |
| ID621 | 0.711bc | 3.96ab | 18.6b–d |
| WA7977 | 0.707b–d | 3.79a–e | 19.3bc |
| WA8002 | 0.706b–d | 4.04a | 17.4c–g |
| WA8003 | 0.667c–e | 3.79a–e | 17.6c–g |
| Bauermeister | 0.661c–e | 3.76a–f | 17.7c–f |
| Eltan[b] | 0.653c–e | 3.81a–e | 18.1b–d |
| Hatton | 0.642de | 3.55d–i | 19.1b–d |
| Darwin[c] | 0.634ef | 3.41f–j | 20.1b |
| AgriPro Palomino[c] | 0.630ef | 3.67b–g | 18.5b–d |
| WA8004[c] | 0.618e–g | 3.66b–g | 17.0d–h |
| ACS51084 | 0.602e–g | 3.87a–d | 15.8e–j |
| MDM[c] | 0.602e–g | 3.95a–c | 15.4g–j |
| WA7976 | 0.567f–h | 3.46e–i | 17.0d–h |
| AgriPro Paladin | 0.558g–i | 3.19ij | 17.9c–e |
| KKHWWW05[c] | 0.558g–i | 3.74a–f | 15.3g–j |
| Weston | 0.533hi | 3.56d–h | 15.6fg–j |
| WA7975 | 0.525hi | 3.29h–j | 17.0de–h |
| ID641[c] | 0.517hi | 3.55d–i | 14.8ij |
| WA8001 | 0.514hi | 3.36g–j | 15.8e–i |
| W98344 | 0.497ij | 3.48e–i | 14.8h–j |
| ORN00B553 | 0.496ij | 3.25h–j | 15.8e–j |
| ORN00B507 | 0.442kj | 3.29h–j | 14.7ij |
| Eddy | 0.401k | 3.70a–g | 11.7k |
| ORN980995 | 0.390k | 3.09j | 13.6j |
| $LSD_{(0.05)}$[d] | 0.059 | 0.30 | 1.9 |

[a] Values followed by the same letter are not significantly different ($P < 0.05$).
[b] Soft white winter wheat.
[c] Hard white winter wheat.
[d] LSD, least significant difference.

**TABLE V**
**Water-Extractable (WE-AX), Total Arabinoxylan (AX), and WE-AX as a Percentage of Total AX (WE/Total) of U.S. Pacific Northwest Hard Spring Wheat Genotypes[a]**

| Genotype | WE-AX (%) | Total AX (%) | WE/Total |
|---|---|---|---|
| Hollis | 0.919a | 4.25b–e | 21.6a |
| WA7954 | 0.877ab | 4.29b–e | 20.5ab |
| Blanca Grande[b] | 0.875ab | 4.57ab | 19.3bc |
| BZ999-339 | 0.868a–c | 4.69a | 18.6b–d |
| WB926 | 0.849b–d | 4.28b–e | 19.9a–c |
| WA7953 | 0.818c–e | 4.30b–e | 19.0b–d |
| Macon[b] | 0.806d–f | 4.39a–d | 18.4c–e |
| Tara2002 | 0.796d–f | 4.34a–d | 18.3c–e |
| Winchester | 0.785e–g | 4.38a–d | 18.0c–f |
| WQL9HDALP[b] | 0.769e–h | 4.70a | 16.4fg |
| BZ9M03-1044 | 0.766e–h | 4.18b–e | 18.5cd |
| WA8017 | 0.756f–h | 4.03de | 18.9b–d |
| WA7998 | 0.754f–h | 4.08c–e | 18.5cd |
| BZ903-455WP-D[b] | 0.731g–i | 4.26b–e | 17.3d–f |
| WA8010[a] | 0.716hi | 4.14c–e | 17.3d–f |
| WA8015 | 0.693i | 4.20b–e | 16.5ef |
| Scarlet | 0.613j | 4.18b–e | 14.6h |
| Otis[b] | 0.596jk | 4.21b–e | 14.2h |
| WA8016 | 0.593jk | 4.28b–e | 13.9h |
| WA7990[b] | 0.586jk | 4.09c–e | 14.4h |
| WA8012[b] | 0.583jk | 4.01de | 14.7gh |
| WA8018 | 0.581jk | 4.02de | 14.4h |
| ID377s[b] | 0.568jk | 4.02de | 14.2h |
| ACS52610 | 0.539k | 4.44a–c | 12.1i |
| Alta Blanca[b] | 0.476l | 3.94e | 12.1i |
| $LSD_{(0.05)}$[c] | 0.051 | 0.33 | 1.7 |

[a] Values followed by the same letter are not significantly different ($P < 0.05$).
[b] Hard white spring wheat.
[c] LSD, least significant difference.

Oregon, and no. 7 in Washington), Hank (no. 5 in Idaho, no. 2 in Washington), and Buck Pronto (no. 3 in Washington) were not included in the present study (none were grown as part of the WSUCVT program nurseries in 2006). The leading hard white spring wheat cultivars of the last two crop years (2006 and 2007) included Klasic, Blanca Grande, Snow Crest, and Pristine. It should be noted that, together, these four cultivars represented only ≈28 kha/year (Idaho and Washington). Blanca Grande was the only one of these four included here but was near the top rank for all arabinoxylan fractions (Table V).

For total AX, the range extended from 3.94% for Alta Blanca up to 4.70% for WQL9HDALP (Table V). Interestingly, both of these genotypes are hard white wheat; WQL9HDALP is a *Pina-D1a/Pinb-D1b* hard near-isogenic line (NIL) of Alpowa soft white spring wheat (Morris 2002; Morris and King 2008). According to DMRT, there were fewer genotype differences for total AX among the hard spring wheats. WQL9HDALP and BZ999-339 were significantly higher than all other genotypes, except the five other genotypes (Blanca Grande, ACS52610, Macon, Winchester, and Tara2002) in the DMRT a group.

The proportion of total AX that was water-extractable ranged from a low of 12.1% for Alta Blanca up to 21.6% for Hollis, again a nearly twofold difference (Table V). Alta Blanca and ACS52610 were significantly lower than all other spring wheats. There then followed a group (DMRT h) that was distinct from nearly all other genotypes. This group was bounded by WA8016 at 13.9% and WA8012 at 14.7%. With the exception of ID377s, all these genotypes are from the Washington State University spring wheat breeding program. The lowest genotype of the higher group was WQL9HDALP and, above the aforementioned break point; it started the DMRT f group.

As a last step in examining the variation among hard winter and spring wheat genotypes of the Pacific Northwest, frequency distributions were constructed (Figs. 1–3). The WE-AX (Fig. 1) distributions exhibited considerable overlap between the winter and spring wheats, with the spring wheats clearly being, on average, higher. Among the winter wheats, there was no clear indication of any non-normal distribution. Among the spring wheats there appeared to be a distinctly bimodal distribution, with frequency maxima at the 0.55–0.6 and 0.75–0.8% class intervals and a minimum between the 0.6–0.65 and 0.65–0.7% classes. It will be of particular interest to test this result with more detailed genetic studies. The distribution of total AX illustrated the nearly complete separation of the winter and spring wheat genotypes (Fig. 2). In actuality, winter and spring wheats overlapped only over a narrow range of 3.94% (Alta Blanca) to 4.04% (WA8002). This marked difference between genotype sets may be due simply to the later heading, grain filling, and maturation typical of spring wheats, or the difference may be related to the specific locations included here or genetic differences between these two genotype sets. Of these three possibilities (there are undoubtedly others), the first strikes us as the most likely; however, this speculation will require additional research. The calculation of WE-AX as a function of the total AX provided a unique perspective on wheat grain arabinoxylan content (Fig. 3). Even though the total AX differed markedly between the winter and spring genotype sets, the ranges for percent WE-AX of the total AX was nearly identical; that is,

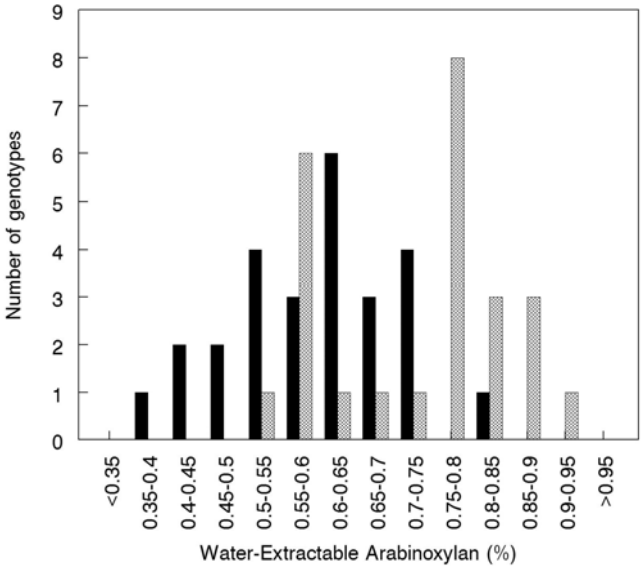


**Fig. 1.** Frequency distribution histogram of water-extractable arabinoxylan from grain of hard winter (solid bars) and hard spring (grey bars) wheat genotypes from the U.S. Pacific Northwest. Genotype means over three locations and two replicates for each growth habit set (winter and spring).

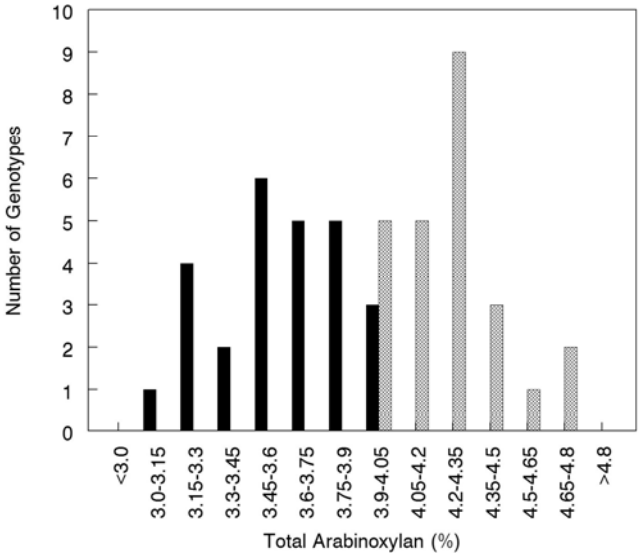


**Fig. 2.** Frequency distribution histogram of total arabinoxylan from grain of hard winter (solid bars) and hard spring (grey bars) wheat genotypes from the U.S. Pacific Northwest. Genotype means over three locations and two replicates for each growth habit set (winter and spring).

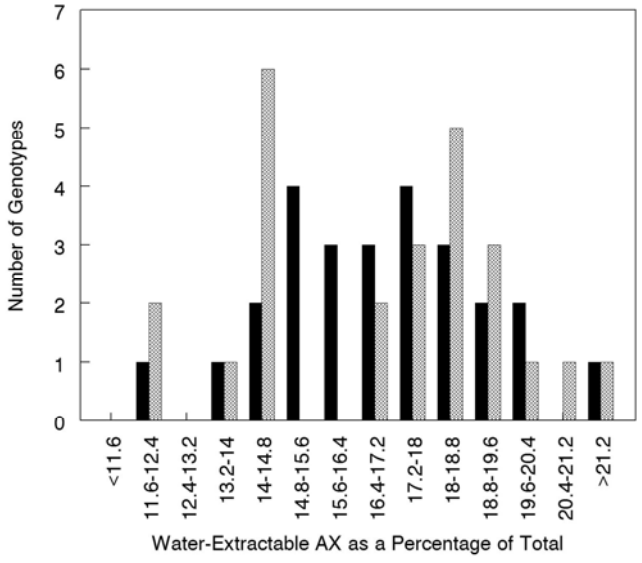


**Fig. 3.** Frequency distribution histogram of water-extractable arabinoxylan (AX) as a percentage of total arabinoxylan from grain of hard winter (solid bars) and hard spring (grey bars) wheat genotypes from the U.S. Pacific Northwest. Genotype means over three locations and two replicates for each growth habit set (winter and spring).

even though spring wheats had more total AX, the proportion that was water-extractable had a similar range (≈11–21%). Among the winter wheats, a less-than-normal distribution may be indicated; certainly the presence of very low (11.6%, Eddy) and very high (21.4%, Juniper) winter genotypes was highlighted. Among the spring wheat genotypes, the distribution was discontinuous and three distinct groupings were apparent. Two genotypes, ACS52610 and Alta Blanca, were low and similar to Eddy hard red winter. At the high end, Hollis hard red spring was similar to Juniper hard red winter. Again, it will be of particular interest to see if these classes are due to genes directly involved in arabinoxylan biosynthesis or postbiosynthetic modification that affects solubility (for example, cross-linking).

## DISCUSSION

Genetic differences exist among wheat genotypes for arabinoxylan fractions. For WE-AX, total AX, and the proportion of total AX that is water-extractable, ANOVA models returned significant genotype effects (Table I) and DMRT identified significant differences among individual hard winter and hard spring genotypes (Tables IV and V). Previous studies have also identified genotype differences in arabinoxylan content of grain (Hong et al 1989; Saulnier et al 1995; Martinant et al 1998; Ordaz-Ortiz et al 2005; Zhang et al 2005; Finnie et al 2006; Barron et al 2007; Jiang et al 2007; Dornez et al 2008a). The environment can play a large role in the variation in arabinoxylan content of wheat, often being an order of magnitude or more greater than that contributed by genotype (Table I). Yet, at other times, for example the total AX content of spring wheat (Table I), the contribution from environment to variation was not significant. As we have observed for other quality traits such as flour-swelling volume (Morris et al 1997), and as Williams et al (2008) aptly stated in their recent review, "Variation in the relative contributions of G, E, and G × E was highly dependent on the G and E sampled." This statement is clearly supported by the different results obtained between the winter and spring wheat sets (Tables I and II) where three otherwise markedly different spring wheat environments did not produce differences in total AX content.

The method of AX measurement should be considered. As part of the review process of this research, a subset of 12 samples were reanalyzed in duplicate with repeated measures using the unmodified Douglas (1981) method. Results of that experiment indicated identical results of WE-AX (data not shown) but some difference in total AX. The Douglas (1981) method modified by Finnie et al. (2006) produced, on average, ≈18% lower values than did the unmodified Douglas (1981) method. The reason or reasons for the slightly lower values are not known. Hashimoto et al (1987) adjusted AX measurements for extraction efficiency. No adjustment was attempted here. Nevertheless, all genotype and environment comparisons and correlations presented here are considered valid.

As a group, the spring wheat genotypes were markedly higher in total AX. Several reasons may account for this difference. Although the most likely may be differences in climatic conditions that winter and spring wheats experience due to the later heading and grain filling of spring wheats, we must also consider that the differences are based in genetics. Certainly, due to practical considerations of plant breeding, the winter and spring wheat gene pools are largely separate and distinct. Of the possible grain traits, including protein, test weight, and SKCS hardness, SKCS hardness had the highest correlation with AX fraction but only within the spring set. Negative correlations ($r$ = –0.46 and –0.51) with WE-AX and proportion of total AX that is water-extractable suggests that harder genotypes have less AX that is water-extractable. Whether this phenomenon is contributing to harder kernels or whether it is simply circumstantial will require additional studies. U.S. hard spring wheats vary in hardness due to different puroindoline mutations, whereas nearly all U.S. hard winter wheats share the same *Pinb-D1b* allele (Morris et al 2001; Morris 2002). Generally, the ranges observed for arabinoxylans of winter and spring wheats were similar (Tables IV and V; Figs. 1–3) and the proportion of total AX that was water-extractable (regardless of the absolute quantity of grain) was similar between winter and spring wheat sets (Fig. 3).

Studies have indicated that management inputs such as nitrogen fertilizer and fungicides have little bearing on arabinoxylan content of grain (Coles et al 1997; Lempereur et al 1997; Dornez et al 2008b), although Li et al (2002) and Wang et al (2006) found otherwise. Drought during grain filling, however, did influence arabinoxylan content (Coles et al 1997). It appears that, once the grain is mature, the arabinoxylan content of the grain is fixed and will only change if sprouting occurs; in this case, endoxylanases hydrolyzing water-unextractable arabinoxylan and rendering it water-extractable (Dornez et al 2008b).

Specific genotypes were identified (Tables IV and V) that may be valuable for additional studies, including those aimed at unraveling the underlying genetics and biosynthesis of arabinoxylans in wheat. Juniper hard red winter genotype was significantly higher than all other winter wheats for WE-AX and ranked highest for percentage of WE-AX of total AX. Eddy and ORN980995 were lowest for WE-AX. For total AX, there were multiple winter genotypes in the high and low DMRT groups, although ORN980995 was again the lowest ranked. For percentage of WE-AX of total AX, Eddy and ORN980995 were again in the lowest DMRT group, with Eddy as the lowest ranked genotype.

Among the spring wheats, Hollis ranked highest for WE-AX and WE-AX as a percentage of total AX. Alta Blanca was significantly less than all other spring genotypes for WE-AX and ranked lowest for total AX and percentage of WE-AX of total AX. The hard NIL, WQL9HDALP, was the highest ranked spring wheat for total AX; Finnie et al (2006) found that the soft, parental NIL, Alpowa, was also the highest in WE-AX and highest ranked genotype for total AX. Blanca Grande hard white spring wheat ranked high for WE-AX, total AX, and WE-AX as a percentage of total AX. Some caution should be used in employing this genotype as a parent because it carries late-maturity α-amylase (LMA) (C. F. Morris and D. A. Engle, data not shown).

In conclusion, this and previous studies clearly indicate that genetic differences exist among wheat genotypes for arabinoxylan fractions. Although arabinoxylans can be highly influenced by environment, a breeding objective of increasing or decreasing the amount of WE (absolute quantity or proportion of total) and total arabinoxylan in wheat grain appears reasonable.


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